

Experimental evidence indicates that native freshwater fish outperform introduced *Gambusia* in mosquito suppression when water temperature is below 25°C

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Abstract In a series of laboratory trials, we compared the mosquito larvae predation efficacy of four endemic fish species and the introduced *Gambusia holbrooki* at different temperatures. *Galaxias occidentalis* and *Galaxias truttaceus*, consumed more mosquito larvae at 15 and 20°C and were equally effective consumers of mosquito larvae as *G. holbrooki* at 25°C. *Nannoperca vittata* and *Bostokia porosa* were equally as effective at consuming mosquito larvae as *G. holbrooki* at 15, 20 and 25°C. *G. occidentalis* in particular warrant further investigation as a mosquito control agent, not only due to their high consumption of mosquito larvae, but also due to their propensity to kill, but not consume more mosquito larvae than the other four fish species at both 15 and 20°C. For this species, stomach size and digestion rate do not appear to limit the number of mosquito larvae killed. These results indicate that

endemic fish species may be more successful than the introduced *G. holbrooki* at mosquito control.

Keywords Mosquito · Predation · Fish · *Gambusia* · *Galaxias* · *Nannoperca*

Introduction

Despite a lack of research quantifying their effectiveness as a biological control agent for mosquitoes, in the early 1900s international health authorities and philanthropic organisations introduced Eastern *Gambusia* (*Gambusia holbrooki* Girard, 1859 Poeciliidae) or Western *Gambusia* (*Gambusia affinis* Baird & Girard, 1853 Poeciliidae) to all continents except Antarctica (Courtenay & Meffe, 1989; Lloyd, 1990). In 1934, without any prior evaluation of endemic fish species, *G. holbrooki* was introduced to Western Australia and distributed by the Public Health Department to prevent the spread of mosquito-borne disease (Mees, 1977). This species is now widespread throughout the southwest of the State (Morgan et al., 1998), particularly in urban areas where they are now found in 63% of natural waterbodies and most artificial lakes (Major, 2009; Hourston et al., 2014). *G. holbrooki* also has a colonizing life history (i.e. early maturation, high reproductive effort) that enables them to rapidly populate a waterbody (Macdonald & Tonkin, 2008). This combined with their agonistic behaviour has contributed to the loss of

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endemic fish species (Myers, 1965; Coy, 1979; Gill et al., 1999) and has led to them now being the most abundant freshwater fish species on the Swan Coastal Plain, where they represent 79% of the total fish abundance in this region (Hourston et al., 2014). However, despite the wide distribution and abundance of *Gambusia*, in south-western Australia the incidence of mosquito-borne diseases such as Ross River virus, Barmah Forest virus, Murray Valley encephalitis virus and Kunjin virus has not decreased (Russell, 1998, 2002).

There is evidence to suggest that *G. holbrooki* are not effective at controlling mosquito larvae abundance (Blaustein, 1992). *G. holbrooki*, is a sub-tropical poeciliid originally from Georgia USA with a preferred temperature of 27°C (Coutant, 1977; Lloyd & Tomasov, 1985). However, even in sub-tropical water temperatures (25°C) one Australian endemic species, Crimson-spotted rainbowfish (*Melanotaenia duboulayi* Castelnau, 1878 Melanotaeniidae), has been shown to consume more mosquito larvae than *G. holbrooki* (Hurst et al., 2004). At the same temperature the predation rate of two other endemic species, Australian smelt (*Retropinna semoni* Weber, 1895 Retropinnadae) and Fly specked hardyhead (*Craterocephalus stercusmuscarum* Gunther, 1867 Atherinidae), is similar to that of *G. holbrooki* (Hurst et al., 2004).

In contrast south-western Australia has a temperate climate, so in this environment the impact of *G. holbrooki* upon mosquito larvae may be even further reduced due to their digestive and reproductive physiology. Firstly, at water temperatures below 30°C *G. holbrooki*'s metabolic rate, and in particular food consumption and swimming speed (i.e. ability to capture prey), decrease exponentially (Wurtsbaugh & Cech, 1983; Cech et al., 1985). Furthermore, their digestion rate also decreases with declining water temperature. Hence, the volume of their digestive tract and rate of discharge restricts the number of mosquito larvae they can consume at cooler water temperatures. For example, at 30°C complete discharge of mosquito larvae occurs 3–4 h after ingestion, but at 17–23°C complete discharge does not occur until 5–6 h after ingestion (Sokolov & Chvaliova, 1936). Secondly, in temperate climates, *G. holbrooki* abundance decreases markedly during the cooler months, then rapidly increases after reproduction peaks in mid-summer (Melden, 1951; Brown & Fox, 1966; Penn & Potter,

1991). Consequently, *G. holbrooki* is typically only abundant at water temperatures above 20°C (Rowe et al., 2007). However, in south-western Australia mosquito larvae begin to hatch in spring, when water temperatures are around 10–15°C, well before the peak in *G. holbrooki* reproduction occurs. Furthermore, aside from shallow, unshaded waterbodies, few freshwater habitats in south-western Australia reach water temperatures of 25–30°C or above, except for a brief period in the peak of summer.

For many years there have been anecdotal reports that endemic species from south-western Australia, in particular the Western Pygmy Perch (*Nannoperca vittata* Castelnau, 1873 Nannopercidae), prey upon mosquito larvae (e.g. Coy, 1979). However, this claim has never been experimentally tested for any Western Australian species, let alone quantified to determine which species is the most effective mosquito larvae predator.

The aim of this experiment was to compare the relative mosquito larvae predation rates of four temperate endemic fish species from south-western Australia—Western Pygmy Perch (*N. vittata*), Western Minnow (*Galaxias occidentalis* Ogilby, 1899 Galaxiidae), Spotted Minnow (*Galaxias truttaceus* Valenciennes, 1846 Galaxiidae) and Nightfish (*Bostokia porosa* Castelnau, 1873 Percichthyidae)—with *G. holbrooki* in temperate (15 and 20°C) and tropical (25°C) water temperatures.

Materials and methods

Collection and holding of freshwater fish

N. vittata (mean standard length and SD of 56 ± 2.6 mm, range 50–60 mm; mean weight and SD of 3.78 ± 0.46 g, range 2.99–4.33 g); *G. occidentalis* (mean standard length and SD of 51 ± 4.9 mm, range 47–62 mm; mean weight and SD of 0.87 ± 0.15 g, range 0.73–1.15 g); and *B. porosa* (mean standard length and SD of 69 ± 3.7 mm, range 65–75 mm; mean weight and SD of 5.87 ± 0.80 g, range 5.22–7.19 g) were collected from Helena River (31°56'S 116°25'E) using double-winged and single-winged fyke nets. *G. truttaceus* (mean standard length and SD of 78 ± 11.1 mm, range 67–93 mm; mean weight and SD of 5.25 ± 2.28 g, range 3.20–8.76 g) were

collected from Goodga River (34°56'S 118°4'E) using A-Frame traps. *G. holbrooki* (mean standard length and SD of 29.3 ± 1.8 mm, range 27–32 mm; mean weight and SD of 0.49 ± 0.10 g, range 0.38–0.62 g) were collected from Herdsmans Lake (31°55'S 115°48'E) using scoop nets and A-Frame traps.

Wild collected *N. vittata*, *G. occidentalis*, *G. truttaceus*, *B. porosa* and *G. holbrooki* were transported to The University of Western Australia Aquatic Research Laboratory, Perth in 200 l polyethylene insulated boxes (IceKool, Australia). Immediately upon arrival all fish were immersed in a salt bath (5 g/l of NaCl) for 15 min to remove external pathogens. They were then placed into 10 × 200 l cylindrical tanks (90 cm diameter × 52 cm high; two tanks for each species) each fitted with individual biological filters, UV water treatment and foam fractionators for a 30-day quarantine and acclimation period. During this period all fish were fed bloodworms (Hikari Sales, USA Inc.) a prey of similar body length (BL, mean \pm SD = 8.78 ± 1.02 mm), body width (BW, mean \pm SD = 0.66 ± 0.20 mm) and shape, to instar IV mosquito larvae (BL mean \pm SD = 7.57 ± 0.55 mm, BW mean \pm SD = 0.82 ± 0.12 mm). Each tank was maintained at pH = 7.0–7.4, a salinity of 0–2 ‰, dissolved oxygen 8–10 mg/l, ammonia <0.01 mg/l and a temperature of 16°C. This ensured that the fish were feeding normally and acclimated to the tank environment prior to the commencement of the first 15°C mosquito larvae predation trials. At the conclusion of each temperature trial, fish were returned to the 10 conical tanks and the water temperature within these tanks was gradually increased over a period of 4–5 days to the next test temperature (i.e. to 20°C, then 25°C).

Mosquito larvae

Several serious human diseases including Murray Valley encephalitis virus, Kunjin virus, Barmah Forest virus and Ross River virus, the most common mosquito-borne pathogen in Australia, have all been isolated from the common urban mosquito *Culex quinquefasciatus* (Mackenzie et al., 1994; Russell, 1998). To produce sufficient *C. quinquefasciatus* larvae for this experiment 6 × 1200 l tanks (1.6 m × 1.6 m × 0.5 m) were filled with water 3 months prior to commencing the first mosquito

larvae predation trial. Eggs laid in the tanks by *C. quinquefasciatus* were hatched and larvae reared until the majority had reached instar IV.

Predation upon instar IV larvae was recorded in this study, (in preference to instars I–III), as a key attribute for effective piscivorous control of mosquito larvae is the consumption of later instars. This is because after instar IV the larvae become airborne, but up until this stage is subject to natural mortality that can be as high as 90% (McDonald & Buchanan, 1981).

Experimental design

This study recorded mosquito larvae predation by five fish species at three temperatures (15, 20 and 25°C). Each temperature trial had five replicates per fish species and five control tanks. The five control tanks contained only mosquito larvae to permit natural larval mortality to be recorded.

The laboratory methods used in this study were adapted from those detailed by Homski et al. (1994), Russell et al. (2001), Hurst et al. (2004) and Willems et al. (2005). In this study two 1200 l water baths (1.6 m × 1.6 m × 0.5 m) were constructed and connected to a water heater–chiller (Fish Cooler DBA150, Daeil Cooler Co Ltd, Korea). Into this bath were placed 30 × 10 l tanks each filled with 7 l water from the fish-holding tank system. Thermometers were placed in the tanks and water temperature adjusted to either $15 \pm 0.2^\circ\text{C}$, or $20 \pm 0.2^\circ\text{C}$ or $25 \pm 0.2^\circ\text{C}$ for 48 h before each trial commenced.

Five of each fish species were removed from the 200 l population holding tanks and placed (1 fish/tank) into one of 25 randomly selected 10 l tanks for an acclimation period of 24 h before the commencement of each trial. They were not fed for the ensuing 24 h to standardise hunger levels. After the acclimation period a random sample of mosquito larvae was collected from the 6 × 1200 l larvae culture tanks. The larvae were graded and hand sorted to remove any instar I, II or III larvae and nauplii. Instar IV larvae were then counted and 200 placed into each of the 25 treatment and five control 10 l tanks (a total of 6000 larvae/trial). Lids were placed on each tank and left undisturbed for 24 h (12:12 h light:dark photoperiod). After 24 h, fish were removed from their tanks. Each fish was anaesthetised (Aqui-S 5 mg/l) for 15 min to enable individual standard length (± 1.0 mm) and wet weight (± 0.01 g) to be recorded. Remaining mosquito larvae

in each tank were counted, both dead and alive, and consumption, or in the case of the control tanks natural mortality, calculated.

Statistical analyses

To correct fish predation data for natural mosquito larvae mortality, Abbott's formula (Abbott, 1925) was used to normalise treatment data for each trial with respect to the mortality recorded in the control tanks. Data were then square root transformed to satisfy the assumptions of normality and equal variance. The Shapiro–Wilk test was used to verify the assumption of normality prior to ANOVA. Mosquito larvae predation rates among fish species for each temperature trial were tested by one-way ANOVA, with all pair-wise comparisons analysed post hoc by Fisher's Least Significant Difference test. (Stat Plus: Mac OS, version 2009, AnalystSoft Inc.).

Results

Fish consumption of fourth instar *C. quinquefasciatus* larvae

The temperate endemic galaxiids (*G. occidentalis* and *G. truttaceus*) consumed more mosquito larvae at both 15°C ($P = 0.04$) and 20°C ($P = 0.01$) than *G. holbrooki*. Furthermore both endemic galaxiids were equally effective consumers of mosquito larvae compared to *G. holbrooki* at tropical temperatures 25°C ($P = 0.49$) (Table 1). *N. vittata* and *B. porosa* were equally as effective at consuming mosquito larvae as *G. holbrooki* at 15, 20 and 25°C ($P = 0.49$) (Table 1).

Table 1 Mean number of fourth instar *C. quinquefasciatus* larvae (expressed as Abbotts adjusted (\pm SD) for natural mortality) consumed over 24 h by four native fish species and *G. holbrooki* at 15, 20 and 25°C

| Fish species | 15°C | 20°C | 25°C |
|------------------------|----------------------------|----------------------------|--------------------------|
| <i>G. occidentalis</i> | 58.0 ^a (52.1) | 73.9 ^a (54.8) | 35.8 ^a (44.1) |
| <i>G. truttaceus</i> | 25.9 ^{a,b} (29.8) | 82.1 ^a (64.6) | 45.8 ^a (64.7) |
| <i>N. vittata</i> | 7.9 ^b (11.1) | 35.7 ^{b,c} (39.8) | 26.5 ^a (23.3) |
| <i>B. porosa</i> | 2.4 ^b (5.7) | 16.7 ^c (28.9) | 14.2 ^a (16.4) |
| <i>G. holbrooki</i> | 16.8 ^b (9.3) | 34.7 ^{b,c} (17.6) | 43.1 ^a (51.9) |

^{a,b,c} Column means followed by the same letter were not significantly different ($P > 0.05$)

Effect of fish size upon consumption of fourth instar of *C. quinquefasciatus* larvae

At 15°C *G. occidentalis* consumed more mosquito larvae per mm of its SL ($P = 0.02$) than *G. truttaceus*, *N. vittata*, *B. porosa* and *G. holbrooki* (Table 2). However, when water temperature increased to 20°C the difference among species diminished (although still significant $P = 0.01$) due largely to increased consumption per mm SL by *N. vittata* and *G. holbrooki*. By 25°C all fish consumed similar numbers of mosquito larvae per mm SL ($P = 0.07$) (Table 2).

At 15°C *G. occidentalis* consumed more mosquito larvae per g bodyweight ($P = 0.003$) (Table 3). At 20°C the difference in consumption/g body weight decreased between *G. occidentalis* and *G. holbrooki* ($P = 0.40$), but was still significant among species ($P < 0.00$). At 25°C *G. holbrooki* consumed more mosquito larvae/g than the other species ($P < 0.05$), but as shown by the large SD consumption was highly variable among individuals (Table 3).

Fish consumption versus predation of fourth instar *C. quinquefasciatus* larvae

The number of dead mosquito larvae in each tank at the conclusion of each trial showed that in addition to consuming large numbers of mosquito larvae, *G. occidentalis* killed, but did not consume, more mosquito larvae than the other four fish species both at 15°C ($P = 0.02$) and 20°C ($P < 0.000$) (Table 4). At these temperatures there was no difference in the number of dead mosquito larvae from natural mortality (control) tanks or those containing the other four fish species (Table 4).

Discussion

The use of larvivorous fishes is one of the oldest methods for biological control of mosquito larvae populations. Despite this there are relatively few controlled studies comparing fishes predation efficiency at the range of temperatures at which mosquito larvae survive. While there are numerous studies on the use of fish to control mosquito larvae, in general the lack of a standardised approach limits comparison among fish species. The benefit of the experimental design in this study is that it permits direct comparison

Table 2 Mean number of fourth instar *C. quinquefasciatus* larvae (expressed as Abbots adjusted (\pm SD) for natural mortality) consumed per mm SL (Standard Length) over 24 h by four native fish species and *G. holbrooki* at 15, 20 and 25°C

| Fish species | 15°C | 20°C | 25°C |
|------------------------|--------------------------|------------------------------|--------------------------|
| <i>G. occidentalis</i> | 1.16 ^a (1.00) | 1.43 ^a (1.10) | 0.75 ^a (0.42) |
| <i>G. truttaceus</i> | 0.34 ^b (0.45) | 1.08 ^{a,b} (0.87) | 0.62 ^a (0.94) |
| <i>N. vittata</i> | 0.14 ^b (0.20) | 0.65 ^{a,b,c} (0.73) | 0.48 ^a (0.41) |
| <i>B. porosa</i> | 0.03 ^b (0.20) | 0.25 ^c (0.43) | 0.20 ^a (0.24) |
| <i>G. holbrooki</i> | 0.57 ^b (0.32) | 1.18 ^a (0.61) | 1.44 ^a (1.68) |

^{a,b,c} Column means followed by the same letter were not significantly different ($P > 0.05$)

Table 3 Mean number of fourth instar *C. quinquefasciatus* larvae (expressed as Abbots adjusted (\pm SD) for natural mortality) consumed per g of fish bodyweight over 24 h by four native fish species and *G. holbrooki* at 15, 20 and 25°C

| Fish species | 15°C | 20°C | 25°C |
|------------------------|----------------------------|----------------------------|-----------------------------|
| <i>G. occidentalis</i> | 67.45 ^a (56.89) | 84.73 ^a (60.52) | 39.25 ^b (48.01) |
| <i>G. truttaceus</i> | 6.09 ^b (9.61) | 18.61 ^b (17.20) | 11.35 ^b (19.34) |
| <i>N. vittata</i> | 1.93 ^b (2.84) | 9.72 ^b (11.35) | 7.58 ^b (6.94) |
| <i>B. porosa</i> | 0.41 ^b (1.01) | 3.07 ^b (5.06) | 2.24 ^b (2.74) |
| <i>G. holbrooki</i> | 34.00 ^b (15.55) | 72.04 ^a (39.15) | 92.97 ^a (103.31) |

^{a,b} Column means followed by the same letter were not significantly different ($P > 0.05$)

Table 4 Mean number dead, but not consumed, of fourth instar *C. quinquefasciatus* predated upon over 24 h by four native fish species, *G. holbrooki* and control at 15, 20 and 25°C

| Fish species | 15°C Mean number dead mosquito larvae (\pm SD) | 20°C Mean number dead mosquito larvae (\pm SD) | 25°C Mean number dead mosquito larvae (\pm SD) |
|------------------------|---|---|---|
| <i>G. occidentalis</i> | 22.60 ^a (22.21) | 27.50 ^a (31.93) | 3.10 ^a (7.08) |
| <i>G. truttaceus</i> | 6.60 ^b (5.08) | 3.40 ^b (7.06) | 4.90 ^a (11.11) |
| <i>N. vittata</i> | 0.00 ^b (0.00) | 0.10 ^b (0.32) | 0.10 ^a (0.32) |
| <i>B. porosa</i> | 2.00 ^b (2.83) | 0.80 ^b (2.53) | 1.80 ^a (2.94) |
| <i>G. holbrooki</i> | 2.80 ^b (4.09) | 3.50 ^b (3.89) | 9.30 ^a (13.63) |
| Control | 2.00 ^b (2.92) | 0.20 ^b (0.63) | 1.60 ^a (4.40) |

^{a,b} Column means followed by the same letter were not significantly different ($P > 0.05$)

of mosquito larvae consumption among fish at 25°C from both northern and southern Australia. The consumption rate by *G. holbrooki* at 25°C (43.1 Instar IV larvae/24 h) recorded in this study is similar to the 41.8 Instar IV larvae/24 h reported by Hurst et al. (2004) at the same temperature. The mean number/g body weight (\pm SD) (92.97 ± 103.31) consumed by *G. holbrooki* in this experiment was less than previously reported at 25°C (121 ± 56.7) (Hurst et al., 2004), but this may be due to the high variation among

individuals. Further research into the variation in mosquito larvae consumption among fishes at different temperatures, as undertaken in this study, will provide important information for the selection of fish species for stocking in sub-tropical and temperate environments to control mosquito-borne disease.

Furthermore, the results of this study show that, gut contents analysis may underestimate the impact of a fish species upon mosquito larvae populations, through not accounting for the non-consumptive

impact of fish upon larvae survival. For example, *G. occidentalis* were found to kill, but not consume mosquito larvae. This contrasts with other species such as *G. holbrooki* and Pacific blue-eye (*Pseudomugil signifer* Kner, 1865 Pseudomugilidae), which have been found to reach a level of satiation when exposed to the high prey densities and late instar larvae used in this study (Willems et al., 2005). This previously unreported behaviour of *G. occidentalis*, combined with their high level of mosquito larvae consumption and ability to tolerate a broad salinity and temperature range, make them a promising candidate for control of mosquito larvae to supplement larviciding efforts as part of an integrated vector control programme.

Some authors have proposed that the incidence and geographic range of mosquito-borne diseases will increase in Australia as a result of climate change (Hales et al., 2002; McMichael et al., 2006). However, other authors have suggested that changes in incidence and geographic range of mosquito-borne diseases are more complex and that climate alone is unlikely to be responsible for the southward spread of mosquito-borne disease. For example, human behaviour associated with our society's response to climate change, such as increased domestic rainwater tanks, and other factors including urban stormwater detention wetlands, international travel and entry of vectors via international vessels may also facilitate the spread of mosquito-borne disease (Russell, 1998; Russell et al., 2009).

Our results show that an additional factor—loss of endemic fish biodiversity—may also increase the spread of mosquito vector populations in south-western Australia. For example, while once common on the urbanised Swan Coastal Plain *G. occidentalis*, *N. vittata* and *B. porosa* now only exist in 20, 9 and 7%, respectively, of water bodies in this region (Hourston et al., 2014). The seasonal drying of some previously permanent waterbodies in south-western Australia due to reduced rainfall as a result of deforestation (Pitman et al., 2004), climate change (CSIRO, 2009), increased groundwater extraction (Balla & Davis, 1993), and management practices (Davis & Froend, 1999), has in many cases resulted in the loss of endemic fish populations that naturally consume and control mosquito larvae. This, combined with the propensity to establish artificial urban lakes without consideration for mosquito control by fish or

other methods, is likely to contribute to an increase in the incidence and spread of mosquito-borne diseases. Indigenous fish species may therefore be suitable for stocking artificial waterbodies in urban areas and restocking natural waterbodies to both control mosquitoes and conserve biodiversity by establishing satellite repository populations. Conservation repositories are particularly relevant for the critically endangered *G. truttaceus*, which currently has a severely restricted distribution in the extreme south of the state, but is not constrained to this region by temperature.

For endemic fish species to provide a viable alternative to *G. holbrooki* for mosquito control, it is essential that adequate numbers of fish are available for stocking. In recent years, our research group have developed techniques for the hatchery production of two species of Galaxias (*G. occidentalis* and *G. truttaceus*) and Western Pygmy perch (*N. vittata*). Ongoing research in this field will determine whether restocking or periodical replenishment will be required in order to use these fish for mosquito control.

In Western Australia, *G. occidentalis* and *G. truttaceus* survive in a wide temperature range (<28°C) and occur in fresh to saline water (0–15 ppt). They belong to the family Galaxiidae, a southern hemisphere, circum-temperate family (McDowall, 2010), that clearly warrants further investigation as a biological control agent for mosquito populations in Australia, New Zealand, South America and Madagascar. Elsewhere in the world where Galaxiidae do not occur naturally, it is likely that other small-bodied endemic fish species have evolved to occupy a similar ecological niche. Our results indicate that if these endemic fish populations have declined or been replaced by *G. holbrooki*, the loss of this biodiversity may contribute to an increase in the transmission of mosquito-borne disease. Further research at both a country and regional scale, to identify and where necessary replenish, these endemic fishes for mosquito control may have benefits for both aquatic biodiversity and human health.

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